

Evolutionary developments in the Silurian Retiolitidae (Graptolites)

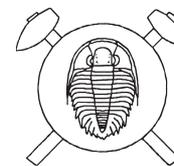
Evoluční rozvoj silurských retiolitidních graptolitů

(3 figs)

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Silurian retiolitid graptolites first appeared during the early part of the Aeronian Stage, and underwent considerable diversification in late Aeronian – earliest Telychian, during which time interval more than thirty species were present globally. A lesser, but significant species peak was again reached in the early Homeric (the *lundgreni* Biozone) prior to the major *lundgreni* extinction event, as a result of which only one species survived. The last retiolitid became extinct during the *leintwardinensis* Biozone (mid Ludlow). The two most striking evolutionary changes, important at the subfamily level, involved the change from outward-facing list seams on the ancora sleeve and smooth or linear striations on the list surfaces (seen in most older forms), to inward-facing seams and lists with a pustulose surface (seen in *lundgreni* Biozone and all younger forms as well as in the older *Sokolovograptus*). Other generalized trends up the stratigraphic column include: loss of preservation of the sicula; more than a twofold lengthening of the sicula; shallowing and decrease in complexity of the ancora umbrella; reduction of the ancora sleeve; change in thecal profile from early orthograptid to later climacograptid; change from a nema attached to the lists throughout, to a nema either attached only distally, often to an appendix, or being a completely “free” nema; development of an appendix in younger forms, and an internal or external nematularium only in some “open-ended” forms; development of the upper apertural list in the early Homeric with complex apertural processes in some forms; marked decrease in size from rhabdosome lengths greater than 100 mm in early forms to two to three millimeters in youngest forms, as well as a tendency towards the simplification of the rhabdosome as expressed in the reduction of thecal and ancora sleeve lists, and accompanied by a marked increase in the length of the sicula.

Key words: Silurian, retiolitids, evolution, list seams, ancora, ancora sleeve

Introduction

The Silurian retiolitids, corresponding to the current restricted use of the Family Retiolitidae Lapworth 1873 (see e.g., Melchin 1998), are a group of graptolites “composed of a network of lists of microfuselli and bandaging, developed from the sicula, nema and thecal walls (thecal framework), and by bifurcation of virgella (ancora sleeve)” (Kozłowska-Dawidziuk 1995, p. 1). In the vast majority of cases, retiolitids are preserved only as a network of lists belonging to the theca framework and ancora sleeve. Except for the earliest taxa, the sicula is rarely preserved. In extremely rare cases, however, very thin fusellar thecal periderm, and ancora sleeve periderm infilling all spaces between the lists of ancora sleeve and the thecal periderm, are preserved (Lenz 1994a; Bates – Kirk 1997; Kozłowska-Dawidziuk 1997, and personal observations Kozłowska-Dawidziuk, Lenz – Melchin 2000). This demonstrates that during their life, all retiolitids, at least in more mature stages, were entirely covered with a periderm and had fully developed siculae, making their relationship to “normal” diplograptids self-evident, although the fusellar layer is extremely thin and the main part of skeleton is cortex that makes up most of the lists. Thus the fusellar layer typical for other graptolites is rarely preserved.

Retiolitids are a complex group, and early efforts at understanding their evolutionary history, using flattened material, have been largely inadequate. The advent of the SEM, and working with isolated, uncompressed ma-

terial, has radically changed the way of looking at retiolitids. Current understanding of the nature of the retiolitid skeleton stems mostly from the studies of Bates – Kirk (1984, 1992, 1997) and Bates (1990). Lenz – Melchin (1987), for the first time, used surface micro ornamentation of rhabdosomal lists to support the division of the retiolitids into Retiolitinae and Plectograptinae. Kozłowska-Dawidziuk (1995) employed a quasi-cladistic approach to divide the retiolitids into five genera-based lineages, and set them into a phylogenetic relationship, using the position of the nema, presence of transverse rods, presence of appendix, and arrangement of ventral and ancora sleeve walls. Lenz – Melchin (1997) carried out a multi-character cladistic study, based on 23 characters, of all genera of retiolitids known at the time; from this they maintained a revised Retiolitinae and Plectograptinae subfamily classification, recognized *Pseudoretiolites* as the primitive stem group, and briefly discussed the major evolutionary developments of the retiolitids. That study, however, was weakened by an inadequate consideration of the specificity of the list ultrastructures as related to individual genera, and of sicula length (as indicated by traces on the virgella). Most recently, Kozłowska-Dawidziuk (2001) proposed the division of the retiolitids into eight phylogenetic lineages each named after a representative genus, including one lineage based on the new genus *Cometograptus*. She recognized the subfamilies Retiolitinae and Plectograptinae using ultrastructural traces on lists to provide information on length of the sic-

ula and thecal pattern, as well as characters from the previous division of the group, to make a new proposal for the evolutionary history and relationships among the retiolitid lineages.

The present paper is an updating and review of the biostratigraphic ranges, and of the general evolutionary patterns seen the retiolitids, based largely on our recent studies of isolated, uncompressed material from Arctic Canada and north-eastern Poland.

Biostratigraphic ranges of retiolitids

In comparison with “normal” graptolites, retiolitids are generally more difficult to recognize or be seen on the rock surfaces when flattened and, when found, they can be difficult to identify with certainty because of their complex morphology. On the other hand, isolated, uncompressed material permits full examination of morphologic complexities, and the specimens can be identified with confidence. Unfortunately, there are relatively few places in the world where long sequences of rocks contain graptolites, including retiolitids, which are preserved in uncompressed form, and can be recovered by acid dissolution of the rocks. Arctic Canada and the Baltic region, including the subsurface of northeastern Poland, stand out as very unique and noteworthy exceptions. In both regions, most of the graptolites are uncompressed and recoverable by acid dissolution providing beautiful preservation as well as a higher diversity than elsewhere and, moreover, these kinds of graptolites range through almost the entire Silurian. As a consequence, the graptolite sequences of these two regions weigh heavily in providing data for taxonomic diversity, and for the lower and upper ranges of the retiolitids shown in Figure 1 (see Eisenack 1951; Lenz 1982, 1988, 1993, 1994b; Lenz – Melchin 1987, 1991; Kozłowska-Dawidziuk 1990, 1991, 1995, 1997, 1999, 2001; Lenz – Kozłowska-Dawidziuk 2001, 2002a). Numerous additional data have, in addition, been gleaned from the studies of mostly flattened retiolitids from elsewhere. These include the studies of Elles – Wood 1908; Bouček – Münch 1943, 1952; Huo 1957; Bjerreskov 1975; Rickards 1976; Lenz 1982; Chen 1984; Obut – Zaslavskaya 1986; Melchin 1989; Ge 1990; Jaeger 1991; Lenz – Melchin 1991; Bates – Kirk 1992, 1997; Rickards et al. 1995; Kozłowska-Dawidziuk, Lenz – Štorch 2001). The biozonal scheme used in Figure 1 is the so-called “simplified graptolite zonal sequence” of Koren et al. 1995.

The earliest retiolitid, *Pseudoretiolites*, appears in the mid-Aeronian (Middle Llandovery) *triangulatus-pectinatus* Biozone (Fig. 1). By comparison, reputed retiolitid ancestors such as *Pseudorthograptus obuti*, or some other ancora-bearing petalolithid (see Rickards – Koren 1974; Bates – Kirk 1992; Melchin 1998), appeared in the underlying *cyphus* Biozone, suggesting that the appearance of the first true retiolitid could not have been much earlier than its presently known first occurrence. Further-

more, *Hercograptus* Melchin (1999), a genus bearing both petalolithid and retiolitid characteristics and a probable sister group to the retiolitids, occurs in the *cyphus* and *triangulatus-pectinatus* biozones. “*Rotaretiolites*” and “*Paraplectograptus*” (undescribed genera as used in Lenz – Melchin 1997), which like *Pseudoretiolites*, have ancora umbrellas that are deep and bowl-like with spiral lists, appear in the *convolutus* Biozone, but are short-lived. True *Rotaretiolites*, which has a shallow, but also spiral-bearing ancora umbrella (Fig. 3.11), is known only in the lower part of the Telychian. This genus is exceptional for a biostratigraphically early form in that it lacks an ancora sleeve (Bates – Kirk 1992). *Pseudoplegmatorgraptus*, a taxon with a shallow, but relatively weakly spiralled ancora umbrella and, uniquely, a double ancora sleeve, first occurs in the uppermost Aeronian *sedgwicki* Biozone, and ranges through to almost the top of the Telychian.

The lower part of the Telychian witnesses the apparently simultaneous appearances of four long-ranging and important taxa, *Retiolites*, *Paraplectograptus*, *Stomatograptus*, and *Sokolovograptus*, each of which is marked by very distinct and different morphological characteristics – for example, the first three genera may possess a nematularium and stomata, while *Sokolovograptus* lacks both – and each is comprised of several or more species.

The late Aeronian to early Telychian appears, then, to have been a time of considerable retiolitid innovation. Furthermore, when the number of species is factored in, the evolutionary “burst” is impressive. Each of the genera *Pseudoretiolites*, *Pseudoplegmatorgraptus*, *Retiolites*, *Paraplectograptus* / *Pseudoplectograptus*, *Sokolovograptus* and *Stomatograptus* (including *Sinostomatograptus*) is represented by three to six species, and “*Rotaretiolites*”, “*Paraplectograptus*” and *Rotaretiolites* are each represented by at least one species. The total species diversity in the early part of the Telychian therefore, probably exceeded thirty, coinciding with a similar high diversity of monograptids (e.g., Melchin et al. 1998).

The Sheinwoodian appears to have been relatively quiet, with only *Eisenackograptus*, the earliest member of the very important *Gothograptus* group (see Kozłowska-Dawidziuk, 2001), appearing in the upper Sheinwoodian, *rigidus-perneri* Biozone. The succeeding *lundgreni* Biozone (lower Homerian) represents a crucial time in retiolitid history. *Retiolites*, *Stomatograptus*, *Paraplectograptus*, and *Sokolovograptus* become extinct about midway through the biozone (Lenz – Kozłowska-Dawidziuk 2001) as shown in Poland and Arctic Canada. *Eisenackograptus* ranges only to the top of the biozone prior to its extinction during the “*lundgreni* extinction event” (Koren 1991).

The *lundgreni* Biozone is uniquely marked by the appearance and proliferation of a new element, *Comeptograptus*, of which there are six species in Arctic Canada, and two different species in north-eastern Poland

(Kozłowska-Dawidziuk 2001; Lenz – Kozłowska-Dawidziuk 2002a), all of which become extinct at the end of the biozone. Finally, and most importantly, the *lundgreni* Biozone witnesses the appearance of *Gothograptus*, the only retiolitid taxon to survive the extinction event (Kozłowska-Dawidziuk 1990) and which was, probably, ancestral to all subsequent retiolitids. *Gothograptus* ranges to at least the late Homerian *praedeubeli-deubeli* Biozone (Kozłowska-Dawidziuk et al. 2001). The immediate post-extinction interval, the *nassa-dubius* Biozone, is relatively quiet with only the numerous *Gothograptus nassa*, and a few geographically restricted occurrences of *Spinograptus* in the upper part of the biozone (see Kozłowska-Dawidziuk et al. 2001).

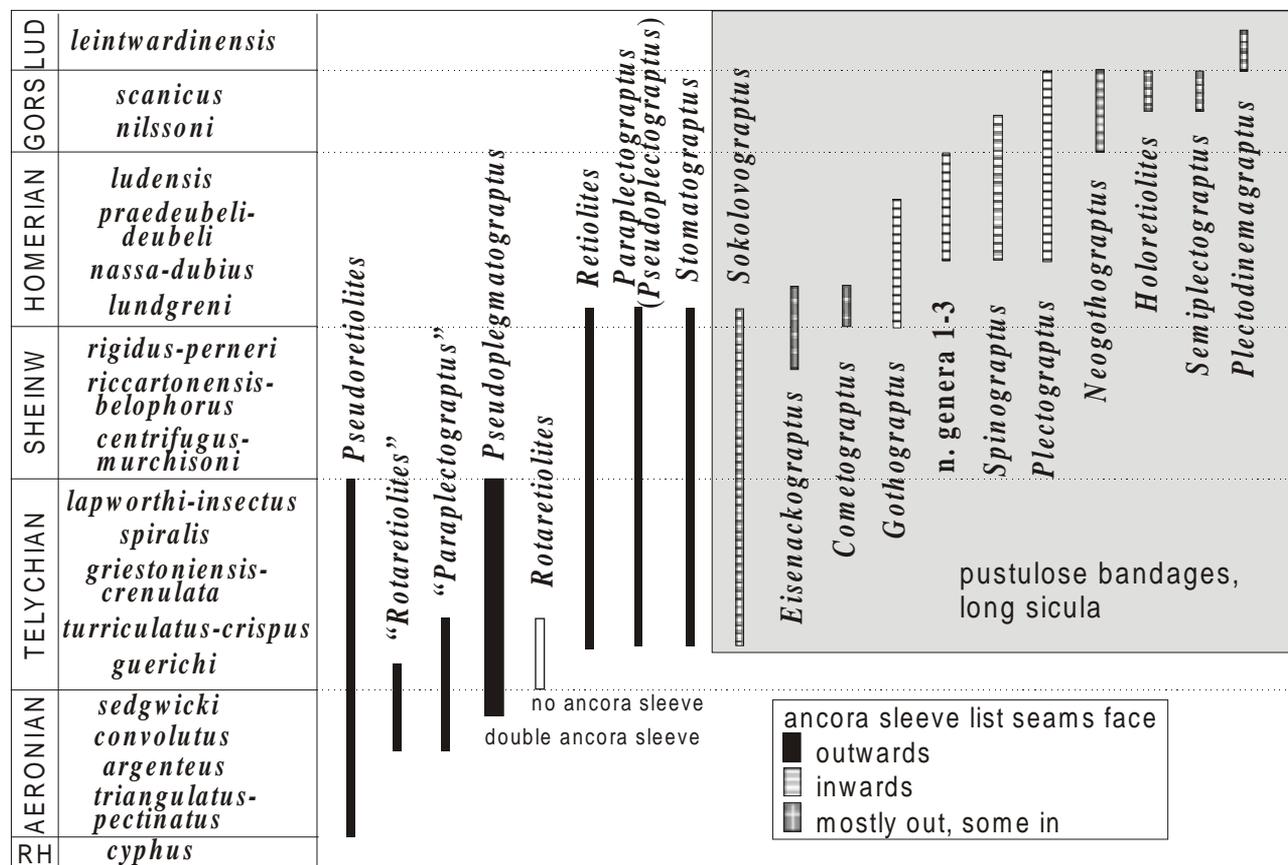
Several new genera with nematularia appeared during the *praedeubeli-deubeli* Biozone, and ranged to the top of the Homerian (described by Lenz – Kozłowska-Dawidziuk 2002a). *Spinograptus*, some forms of which possessed an appendix, became common and widespread at this time and ranged into the lower part of the Lower Ludlow; during this time-range interval it proliferated into five species: *S. clathrospinus*, *S. latespinus*, *S. lawsoni*, *S. reticulolawsoni*, and *S. spinosus*. In the upper half of the upper Homerian, therefore, nine to ten species of retiolitids existed globally (see Lenz – Kozłowska-Dawidziuk 2002b?). *Plectograptus* appears at this

time too, but is rare and apparently geographically restricted.

The Lower Ludlow witnessed the continuation of *Spinograptus*, the widespread distribution and modest proliferation of *Plectograptus* as well as further derivatives such as *Semiplectograptus* and *Plectodinemagraptus*. The latter two are the youngest known retiolitids, found so far only in northeastern Poland (Kozłowska-Dawidziuk 1995). There is also continuation and diversification of the *Gothograptus* lineage as represented by *Neogothograptus* and later *Holoretiolites*. Species diversity reached at least seven or eight during the upper Gorsian, not long before the total extinction of the retiolitids.

The Ludlow witnessed two patterns of rhabdosome development: rhabdosomes that were relatively large and “open-ended” (e.g., *Plectograptus* and at least some *Spinograptus*, both of which sometimes developed nematularia), and those that were relatively small and possessed an appendix (e.g., *Neogothograptus* and *Holoretiolites*). A more or less equal number of species in each subgroup existed during this time. There is, however, very little information on whether one subgroup preceded the other in its disappearance, or whether the two subgroups were extinguished more or less simultaneously. At the moment, *Plectodinemagraptus*, a plectograptid, appears to represent the last surviving retiolitid.

Fig. 1 Biostratigraphic ranges of retiolitid genera, showing position of ancora sleeve list seams, long siculae, and pustulose bandages on lists.



Evolutionary trends in the Retiolitidae

Retiolitid ancestry

There is general agreement that the ancestry of the Silurian retiolitids lays with some Pattern I ancorate petalolithid such as *Petalolithus* or *Pseudorthograptus* (Rickards et al. 1977; Mitchell 1987; Bates – Kirk 1992; Kozłowska-Dawidziuk 1995; Lenz – Melchin 1997; Melchin 1999). The rare occurrence of retiolitids possessing a complete periderm (see Lenz 1994a), and the discovery of a form that immediately pre-dates the earliest retiolitid and possesses characteristics more or less intermediate between the petalolithids and retiolitids (Melchin 1999), adds further strong support to this interpretation. The development of the retiolitids is then perceived to unfold in the following manner, although the actual steps are obscure: beginning with some “normal” petalolithid with a normally-developed periderm and well-developed ancora, the next step was the increasingly distal development of the ancoral lists to the point where they essentially entirely enveloped the thecae. Ventrally and distally, one opposing pair of primary ancora lists divided and lengthened, and were incorporated into the thecal rims and lips, and generally in the lateral parts of the rhabdosome, comprising the thecal framework (Bates 1990). The other pair of opposing primary ancora lists divided and lengthened frequently, but in a less precise way to form a separate layer over the lateral walls. This layer, the ancora sleeve of Bates (1990), lies outside and is separate from the thecal framework list layer, but is ventrally attached to the thecal framework (see Lenz 1994a; Kozłowska-Dawidziuk 1997, Lenz – Thorsteinson 1997). The ancora sleeve is a unique structure, being known only among the retiolitids, and its relationship to the thecae is not fully understood.

List structure and micro ornamentation

Lists are built of microfuselli and bandages that, layer-by-layer, increase in thickness as the rhabdosome matures (Bates 1987). As a result, ancora sleeve lists and thecal lists all possess seams along their lengths. These seams occasionally retain poorly preserved shard-like incremental remnants of the once-continuous fusellar layer (Bates 1987).

List micro ornamentation, in the form of a smooth surface or parallel striations, is characteristically found on the lists of most older retiolitids, including *Pseudoretiolites*, *Pseudoplegmograptus*, *Stomatograptus*, *Retiolites*, “*Rotaretiolites*”, “*Paraplectograptus*” and *Rotaretiolites*. In all of these taxa, the seams of the ancora sleeve are situated on the outside, suggesting that list secretion proceeded from the inside. Beginning with *Paraplectograptus* and *Sokolovograptus*, new micro ornamentation developed in the form of pustules, while ancora sleeve list seams face out and in, respectively. All subsequently appearing retiolitids are more or less pustulose. *Eisenack-*

ograptus appears in the upper Sheinwoodian, and its lists are entirely pustulose; however, while possessing mostly outward facing list seams (in-facing ornamentation), some ancora sleeve list seams are in-facing. *Cometograptus*, confined to the *lundgreni* Biozone, is the youngest-appearing form with mostly outward-facing list seams of the ancora sleeve, but its ornamentation is entirely of weak to strong pustules (Kozłowska-Dawidziuk 2001, Lenz – Kozłowska-Dawidziuk 2002a). The lists of all remaining, younger retiolitids bear pustules and in-facing list seams. *Sokolovograptus* (Figs 3.18, 3.20) is, however, an anomaly in appearing so early (Fig. 1), but in possessing the “advanced” characteristics of inward facing list seams and external pustulose ornamentation. It was possibly ancestral to some of the post-extinction retiolitids, although there is no form that appears to be directly related to *Sokolovograptus* and it may, instead, have been an early, but isolated offshoot.

Sicula preservation

It is clear that retiolitids possessed a fully functional sicula during their lifetime. The retiolitid sicula was, however, a very delicate structure, and was commonly partially preserved only in the earlier retiolitids. The prosicula and part of the metasicula is commonly preserved in *Pseudoretiolites* (Figs 2.6, 2.9), while only the prosicula is preserved in *Pseudoplegmograptus*, “*Rotaretiolites*” and “*Paraplectograptus*” (see Lenz – Melchin 1997). In *Stomatograptus* (Figs 2.10, 2.11) the prosicula is most often preserved, while in *Retiolites* and *Paraplectograptus* it is rarely preserved in full (Kühne 1953; Obut – Zaslavskaya 1976, Kozłowska-Dawidziuk 1995; Bates – Kirk 1997), but may be represented by a thickening or sicula threads (Lenz – Melchin 1987a). *Rotaretiolites* (Fig. 3.11) does not preserve the prosicula, but often retains a complete prosicular ring (Bates – Kirk 1992) and sometimes, a prosicular longitudinal list. A prosicula has been observed in *Sokolovograptus* (Obut – Zaslavskaya 1976), but is an extremely rare occurrence.

Younger retiolitids only occasionally retain fragments of the prosicula ring and/or of a longitudinal list; however, prominent sicular seams visible along the virgella (virga), permit recognition of the position and length of both the prosicula and metasicula (Bates – Kirk 1997, Kozłowska-Dawidziuk 1998). In extremely rare cases where the rhabdosome retains a complete periderm, the sicula is also fully preserved (Lenz 1994a, Kozłowska-Dawidziuk 1997).

Sicula development

Bates – Kirk (1992) and Kozłowska-Dawidziuk (1998) recognized the differing lengths of siculae present in the different groups of retiolitids. Bates – Kirk (1992) recognised two basic size classes, while Kozłowska-Dawidziuk (1998) has recognized three. All but one of the oldest taxa (*Pseudoretiolites*, *Pseudoplegmograptus*,

Rotaretiolites, *Retiolites*, *Stomatograptus*, and “*Paraplectograptus*”) have short siculae (< 1.0 mm). The *Paraplectograptus* (including *Pseudoplectograptus*) group whose age-range overlaps entirely with *Retiolites* and *Stomatograptus*, and *Gothograptus*, have slightly longer siculae (about 1.4 mm). *Eisenackograptus*, appearing in the upper Sheinwoodian, *Cometograptus*, confined to the lower Homerian, and all the youngest forms (*Spinograptus*, *Neogothograptus*, *Plectograptus*, and *Holoretiolites*) have long siculae (2.0–2.5 mm). *Sokolovograptus*, while entirely overlapping in age-range with *Retiolites* and *Paraplectograptus*, also possesses a very long sicula. The fact that *Sokolovograptus* appears so early yet has a long sicula, and inward facing list seams (i.e., “advanced” characteristics), makes it anomalous.

The presence of varying sicula lengths in different taxa has prompted the proposal of a polyphyletic/diphyletic origin of the retiolitids (Bates – Kirk 1992). However, since sicular lengths in general increase up the stratigraphic column, that interpretation is unlikely, or at least, unnecessary.

Ancora development

The ancora umbrella of the earliest retiolitids, like that of some of their purported ancora-bearing petalolithid ancestors, was deep and bowl-shaped (as in *Pseudoretiolites*, Fig. 2.6), and bore a double spiral thread (Bates – Kirk 1984), as did “*Rotaretiolites*” and “*Paraplectograptus*” of Lenz – Melchin (1997). The slightly younger taxon *Rotaretiolites* possessed a simple, shallow ancora umbrella composed of four-pronged ancora lists with single horizontal lists along the rim (Fig. 3.11), but still retained the spiral list structures.

Ancora umbrellas of *Pseudoplegmatoraptus*, *Retiolites* (Figs 2.2, 2.5) and *Stomatograptus* (Figs 2.10, 2.11) were shallow, but the primary ancoral lists further subdivided distally, resulting in a somewhat more complex polygonal pattern, and more complex rims. *Pseudoplegmatoraptus* still retained the double-spiralled threads. Ancora umbrellas of subsequent taxa were relatively shallow and simple: in *Paraplectograptus* and *Sokolovograptus*, the ancora lists bifurcate, but the umbrella is simple and extremely shallow (Fig. 3.20); in a second group such as *Eisenackograptus*, *Gothograptus* and *Spinograptus*, the ancora lists bifurcate and the distal margin of the umbrella possesses somewhat more complex list structures along the rim; and in the youngest group, *Plectograptus*, *Semiplectograptus* and *Plectodinemagraptus*, the umbrella is extremely simple and shallow, and two of the four primary ancora lists that make up the four meshes are usually under-developed (Figs 3.4, 3.9, 3.21).

Ancora sleeve

The ancora sleeve, which is present in almost every retiolitid, is the next stage of development from the ancora umbrella and begins as lists connecting with the first th-

ecae. The first known retiolitids such as the *Pseudoretiolites*, *Pseudoplegmatoraptus*, *Retiolites* and *Stomatograptus* groups possess well-developed ancora sleeves in which the list seams face outwards. The structure is built as a network of thin lists referred to as reticulum. The reticular lists are connected with stronger internal lists belonging to the thecal framework. The maximum of complication of the ancora sleeve development is reached in *Pseudoplegmatoraptus*, where it is developed as two layers: an inner layer with seams on lists facing outwards, and the outer layer with seams on lists facing inwards (Bates – Kirk 1992, 1997). Thus there is a space between the thecal wall and ancora sleeve, as well as a space between two ancora sleeve layers in the rhabdosome. Other older forms such as *Paraplectograptus* and *Pseudoplectograptus* (Figs 2.1, 3.15), often possess much simpler ancora sleeves. A similar model of that structure, composed of thin, mostly irregular lists, occurs in *Sokolovograptus*. In that lineage, some trend towards the thickening and horizontal arrangement of the lists in distal parts of the rhabdosome is observed; furthermore, there is a tendency towards a strong reduction of lists to the point where relatively few lists remain (Kozłowska-Dawidziuk 1995). The difference between *Sokolovograptus* and other older, but coeval forms, is that its list seams face inwards. *Rotaretiolites* is an exception among older forms, in not having developed an ancora sleeve (3.11).

Among species of the *Cometograptus* group, confined to the *lundgreni* Biozone, there is a range of variation in the development of the ancora sleeve from many irregular thin lists as in *Cometograptus apoxys*, to the regular thick lists in *C. tomczyki* (Lenz 1993; Kozłowska-Dawidziuk 2001) (Figs 2.13, 3.8). The most spectacular reduction of the ancora sleeve is, however, observed in the *Gothograptus* lineage. In its first representative, *Eisenackograptus* (Fig. 3.5), the ancora sleeve is built of a dense network of irregular thin lists with list seams facing outwards, while on some thicker lists the list seams face inwards. In succeeding forms such as *Gothograptus*, *Neogothograptus* and *Holoretiolites*, the list seams of the ancora sleeve all face inwards, and they exhibit a tendency towards reduction in the number of thin lists, as well as a further reduction in the number of thicker lists, the so-called clathrium (Figs 3.2, 3.4, 3.17). A similar trend in the reduction of reticular and clathrial lists is observed in the *Spinograptus* and *Plectograptus* lineages, until in the final member – *Plectodinemagraptus gracilis* – there appears to be no ancora sleeve (Figs 3.7, 3.9).

The trend in the reduction of the ancora sleeve up the stratigraphic column is accompanied by a concomitant decrease in the size of entire colony, as well as in the number of thecae. However, the structural development between thecal wall and ancora sleeve wall is still not understood in many forms, particularly in those in which the seam lists face in, although Bates – Kirk (1992, 1997) have made preliminary studies of some of the older forms. As a result, evolutionary trends in many forms are not well understood.

Thecal profile

As already noted, retiolitid thecae were made of extremely thin fuselli and for this reason are normally not preserved; as a result, it is only rarely that the actual thecal walls are observable. Recognition of the thecal profile is possible, however, using traces such as transverse rods and thecal lip position, as well as ventral margin of thecae preserved as lists such as mid-ventral, sigmoidal or inner connecting lists. Exceptionally, some or all of thecal periderm is preserved (Lenz 1994a; Lenz – Thorsteinsson 1997), making thecal profile unequivocal. The thecae of most of the oldest taxa – *Pseudoretiolites*, *Rotaretiolites*, *Pseudoplematograptus*, *Retiolites* and *Stomatograptus* – were clearly orthograptid in profile (Figs 2.2, 2.4, 2.6, 3.16). This is demonstrated by the presence of mid-ventral thecal list in taxa such as *Pseudoretiolites* and *Rotaretiolites*, and by the rare preservation of thecal ventral walls in *Retiolites* and *Stomatograptus* (Holm, 1890; Lenz – Melchin, 1987b; Lenz – Thorsteinsson, 1997). *Paraplectograptus* and *Pseudoplectograptus* probably also exhibited orthograptid thecal profiles (Figs 2.1, 3.15), as shown by the inclined genicular wall posterior of the apertural lip and position of transverse rods in *Pseudoplectograptus sagenus* (Lenz 1993). The thecal profile in *Sokolovograptus* is not clear, but could have been either glyptograptid or climacograptid (Fig. 3.20).

The orthograptid thecal profile disappeared together with the oldest groups of retiolitids during *lundgreni* Event. This was replaced by a climacograptid profile, beginning in the early Homerian (earlier if *Sokolovograptus* possessed a climacograptid profile) with the appearance of the *lundgreni* Biozone forms *Gothograptus* and *Cometograptus*, and continued in all post-extinction retiolitids. The presence of a complete periderm on “*Agastograptus robustus* Obut – Zaslavskaya” described in Lenz (1994a), and on *Spinograptus* (Kozłowska-Dawidziuk 1997) (Fig. 2.3) convincingly demonstrates this. Only *Eisenackograptus* (Fig. 3.5) is unusual in that it clearly possesses thecae with a pseudoglyptograptid pro-

file (Lenz 1994a). Generally speaking, a long sicula and pustular ornamentation accompanied the climacograptid-profile retiolitids. Thecal profile is a feature that confirms the Pattern I (Pattern R of Melchin 1998) astogenetic development of retiolitids.

Virgula/Nema attachment

Internally, the virgula/nema of all older retiolitids from *Pseudoretiolites* to *Stomatograptus* (see Fig. 1) was an integral part of the rhabdosomal framework in being directly joined to the thecal framework (Figs 2.1, 2.2, 2.10). In *Sokolovograptus*, and in *Cometograptus*, *Spinograptus* and *Plectograptus*, and the youngest genera of the *Gothograptus* lineage (*Neogothograptus* and *Holoretiolites*), as well as in new post-*lundgreni* genera (Lenz – Kozłowska-Dawidziuk 2002b?), the virgula/nema appears to be unattached, or only loosely attached to the distal-most parts of the open-ended rhabdosome distal of the ancora (Figs 3.2, 3.4, 3.20, 3.21).

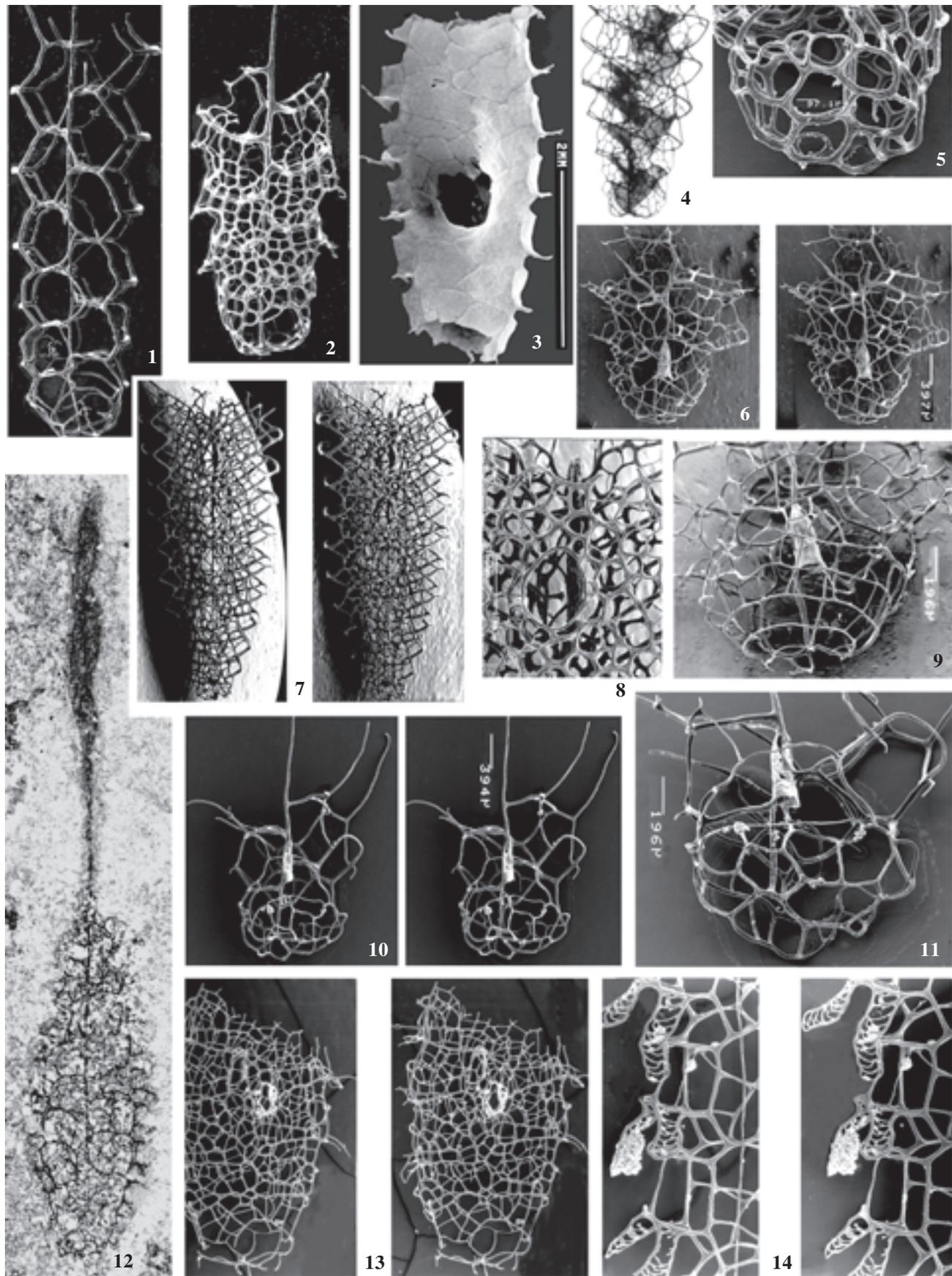
It is interesting to note the trend to loose contact of the nema with the rhabdosomal framework through the *Gothograptus* lineage, the first lineage with a developed appendix. The pre-*lundgreni* forms of this lineage possess a nema fused to the lateral wall of the ancora sleeve, whereas in post-extinction representatives of the lineage, represented by *Neogothograptus* and *Holoretiolites*, the nema has a central position in rhabdosome as it has in every other retiolitid of this interval. The overall trend is thus toward a length-increase in the sicula, and larger central common canal, suggesting a different organisation of the colony.

Appendix and nematularium

A nematularium, as a spiral structure, a one-vane thickening or a three-vane structure, was fairly common among the petalolithids (e.g., see Hundt, 1965; Lenz, 1982). The spiralled nematularium, or a much-thickened nema, was also occasionally present in retiolitids (see



Fig. 2 1 – *Pseudoplectograptus simplex* Kozłowska-Dawidziuk, field designation CP70, 600–625' (183–190.5 m), *rigidus-perneri* Biozone, Arctic Canada, showing attached nema and weak ancora sleeve, SC78441, x18; 2, 5 – *Retiolites* sp., field designation CP70, 450–500' (137–152 m), *lapworthi-insectus* Biozone, Arctic Canada, GSC114221: 2 – showing proximal thecal hoods, attached nema, x23; 5 – enlargement of ancora umbrella; 3 – *Spinograptus* sp., field designation Aba3-98, 21 m, *praedeubeli-deubeli* Biozone, Arctic Canada, showing continuous fusellar periderm, climacograptid thecal profile, and stoma (also present on opposite lateral wall), GSC114222; 4 – *Retiolites* sp., GSC locality number 61746, *spiralis* Biozone?, showing continuous thecal wall periderm, GSC115529, x3; 6, 9 – *Pseudoretiolites* sp., field designation ML64, upper B, *convolutus* Biozone, Arctic Canada, GSC114223; 6 – showing ancora umbrella, sicula, orthograptid thecal ventral walls; 9 – enlargement of ancora umbrella showing spiral structures and prosicula; 7, 8 – *Stomatograptus grandis* Suess, MCP325: 7 – stereopair showing stoma and internal nematularium; 8 – enlargement of stoma and nematularium; 10, 11 – *Stomatograptus* sp., field designation MCP 148, *lapworthi-insectus* Biozone, Arctic Canada, GSC114224: 10 – stereopair showing ancora umbrella and prosicula; 11 – enlargement of ancora umbrella and prosicula; 12 – *Plectograptus? karlsteinensis* Kozłowska-Dawidziuk, Lenz and Štorch, Vs1, 110–120 cm, *praedeubeli-deubeli* Biozone, Všeradice section, Czech Republic, showing spiralled nematularium, PS 956, x6; 13 – *Cometograptus apoxys* (Lenz), field designation SBC 10D, *lundgreni* Biozone, Arctic Canada, stereopair, showing genicular spines, and stomata on both lateral walls of rhabdosome, GSC 99164, x16; 14 – *Spinograptus quadratus* (Lenz), field designation SJF 155 m, *progenitor/nilssoni* Biozone, Arctic Canada, stereopair enlargement of ventral wall showing complex genicular “spines”, GSC99172, x28.



e.g., Kozłowska-Dawidziuk et al. 2001). Although the thickened structure was generally present outside the body of the rhabdosome (Fig. 2.12), it sometimes developed internally (Lenz – Melchin 1987a; Kozłowska-Dawidziuk et al. 2001, Lenz – Kozłowska-Dawidziuk 2002a).

A nematularium has been observed in some older retiolitids such as “*Pseudoplegmatoraptus*” (Štorch 1992), *Stomatograptus*, *Paraplectograptus* and *Pseudoplectograptus* (Figs 2.7, 2.8, 3.15, 3.19) as well as in the younger (lower Homeric, *lundgreni* Biozone) forms. Other older “open-ended” retiolitids (i.e., those without an appendix) probably also possessed nematularia that have not been preserved. Similar nematularia have recently been observed in new genera from post-*lundgreni* interval (Lenz – Kozłowska-Dawidziuk 2002a) and in the Ludlow, as in *Plectograptus macilentus* (Bouček – Münch 1952). Nematularia could have been related to orientation and vertical movement in the water column.

A different way of life is suggested by those retiolitids with an appendix at the end of the rhabdosome. The first forms with an appendix, the members of the *Gothograptus* lineage, appear in the late Sheinwoodian (*Eisenackograptus*), but proliferate in the *lundgreni* Biozone beginning with the appearance of the oldest *Gothograptus*. In the older members of the lineage (*Eisenackograptus* and *Gothograptus*) (Figs 3.4, 3.5), the appendix can be as long as the thecal part of the rhabdosome, whereas in the younger (Ludlow) forms such as *Neogothograptus* and *Holoretiolites* (3.2, 3.16, 3.17), it was normally very short to almost rudimentary, although occasionally in some forms it can be long (Fig. 3.4). An appendix is also sometimes present in some *Spinograptus* (see Lenz, 1994a; Kozłowska-Dawidziuk, 1997).

Apertural processes

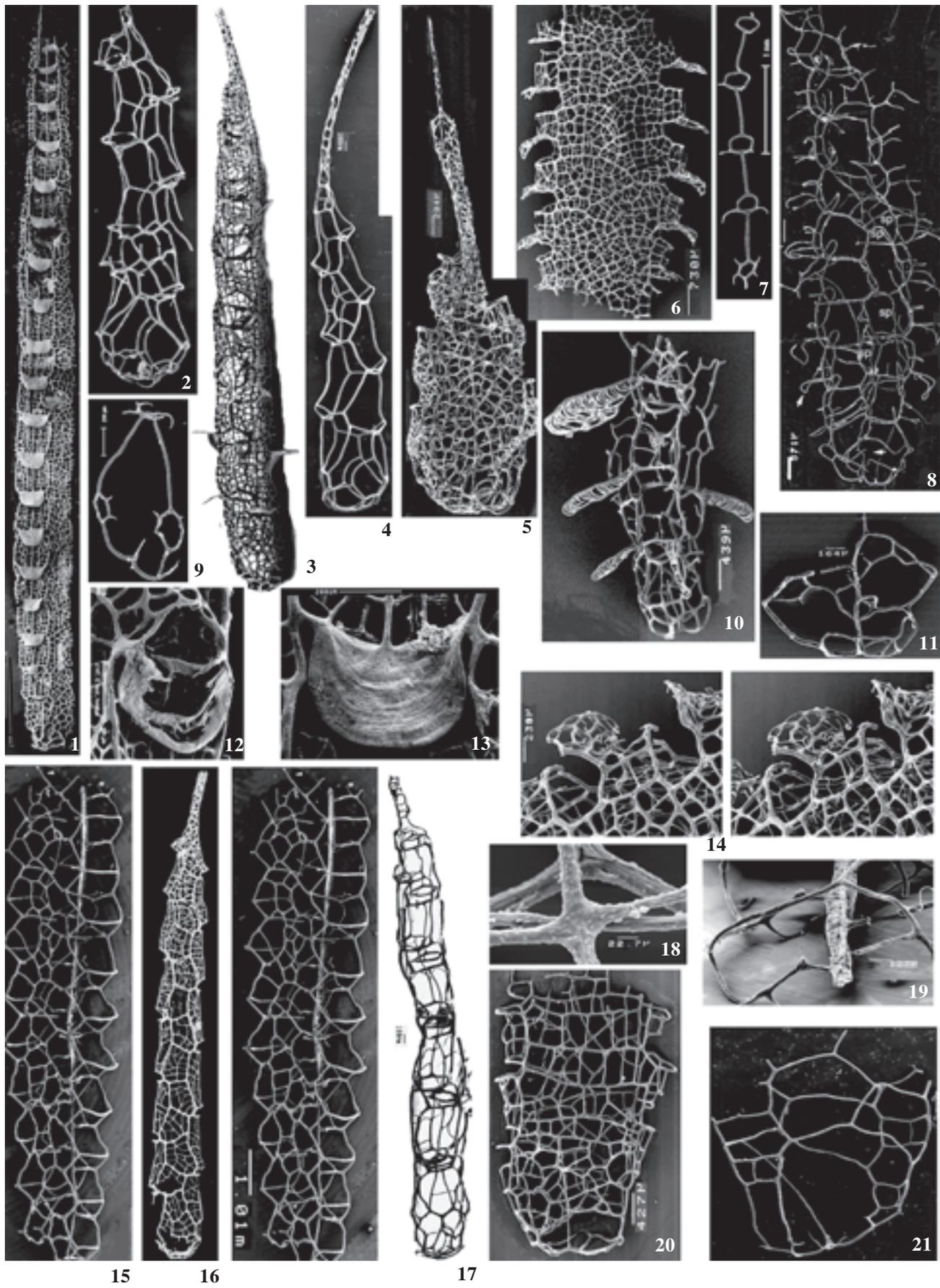
The evolution of apertures in retiolitids occurs in two stages. The oldest types lacked upper apertural lists and in only a few taxa such as *Pseudoplegmatoraptus* and “*Rotaretiolites*”, simple paired spines were present along the lateral margins of the thecal aperture lists. More complex apertural structures in the form of a “thecal hoods” were developed in the first two or three thecal pairs of some specimens of *Retiolites* (Fig. 2.2). Since, however, specimens with and those without thecal hoods occur in the same collections and are otherwise identical, the presence of a thecal hood is considered to be intraspecific variation.

Spines and genicular processes – some very complex – become much more common in younger forms, beginning in the early Homeric, and occur in some species of *Cometograptus* [e.g., *C. tomczyki* (Fig. 3.8), *C. koreni*, and *C. nevadensis*] (see Kozłowska-Dawidziuk 2001). These processes are particularly prominent in *C. apoxys* (Fig. 2.13) in which the supra-apertural genicular processes are complex, well developed, and connected to the ancora sleeve (Lenz – Kozłowska-Dawidziuk 2002b?).

An important new morphological development, the upper apertural list, first appeared within the *Gothograptus* group in the lower Homeric, *lundgreni* Biozone. The appearance of the upper apertural list and accompanying lateral thecal lists permitted the development of a rounded or oval thecal aperture and an array of different kinds of apertural processes. In *G. kozłowskii*, for example, proximal thecae possessed microfusellar hoods, medial thecae bore spines and loops, and distal thecae developed reticular hoods (Figs 3.3, 3.12), whereas in



Fig. 3. 1, 13 – *Gothograptus nasssa* (Holm), Bartoszyce borehole, 1656.8 m, northeastern Poland, *nassa* Biozone, showing well-developed thecal hoods, ZPAL G.29/1: 1 – long specimen, x6.8; 13 – enlargement of thecal hood, showing pustulose bandaging; 2 – *Neogothograptus* sp., field designation SBC4, 7 m, *progenitor* Biozone, Arctic Canada, showing very short appendix, GSC99169, x21; 3, 12 – *Gothograptus kozłowskii* Kozłowska-Dawidziuk, Baltic erratic boulder 147, *lundgreni* Biozone, ZPAL G.XIII/43: 3 – mature specimen showing differing types of thecal hoods and spines, x11; 12 – enlargement of distal thecal hood; 4 – *Holoretiolites mancki*, Baltic erratic, locality Jarosławiec 48, *paracanonicus* Biozone, mature specimen with very long appendix, ZPAL G.28/1; 5 – *Eisenackograptus eisenacki* Obut – Sobolevskaya, field designation AB1-91, 17.5 m, *lundgreni* Biozone, Arctic Canada, short, mature specimen with very long appendix, GSC119779; 6, 14 – *Papiliograptus papilio* Lenz – Kozłowska-Dawidziuk, field designation AB_a3-98, 21 m, *praedeubeli-deubeli* Biozone, Arctic Canada, GSC120731: 6 – mature specimen showing thecal apertures, and complex genicular hoods; 14 – stereopair enlargement of thecae and genicular hoods; 7, 9 – *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, Mielnik borehole, 946.0 m, *hemiaversus* Biozone, northeastern Poland, ZPAL G.XVI/1409 and ZPAL G.XVI/1410: 7 – ventral wall thecal apertures; 9 – ancora and three thecal apertures; 8 – *Cometograptus tomczyki* Kozłowska-Dawidziuk, Bartoszyce borehole, 1663.4 m, *lundgreni* Biozone, northeastern Poland, large specimen showing looped genicular processes (arrow), lateral orifice (arrow) and ancora sleeve spines (sp), ZPAL G. 24/8. *Spinograptus* cf. *latespinosus* Kozłowska-Dawidziuk, field designation SB E142 m, *praedeubeli-deubeli* Biozone, Arctic Canada, showing exceptionally large genicular processes, GSC120739; 11 – *Rotaretiolites exutus* Bates – Kirk, field designation LL1-80, *turriculatus* Biozone?, Arctic Canada, showing simple ancora umbrella, ventral thecal lists and prosicular ring, GSC114225; 15, 19 – *Pseudoplectograptus simplex* Kozłowska-Dawidziuk, field designation SB F3 m, *lundgreni* Biozone, Arctic Canada, GSC114226: 15 – stereopair showing long, internal nematularium; 19 – enlargement and rotation of nematularium showing its three-vented structure; 16 – *Neogothograptus balticus* (Eisenack)?, field designation BH1-91, 57.6 m, *progenitor* Biozone, Arctic Canada, showing long rhabdosome, dense reticulum, and relatively short appendix, GSC104694, x13; 17 – *Neogothograptus balticus* (Eisenack), Baltic erratic boulder 49 Jarosławiec, ventral view of mature rhabdosome with short appendix, ZPAL G. 27/2; 18, 20 – *Sokolovograptus parens* Obut – Zaslavskaya, field designation MRC03-02N, *perneri-opimus* Biozone, Arctic Canada, GSC114227: 18 – enlargement of lists showing pustules, central nema, and list seams; 20 – incomplete mature specimen showing “free” nema, ancora umbrella, and ventral thecal wall lists; 21 – *Plectograptus macilentus* (Törnquist), Baltic erratic boulder 46 Jarosławiec, proximal fragment of immature rhabdosome with three first thecae and simple ancora, ZPAL G. 27/1.



G. obtectus and *G. nassa* (Figs 3.1, 3.13), large thecal hoods were present throughout and often completely hid the thecal apertures. In post-*lundgreni*, upper Homeric retiolitids, apertural processes are common, especially in *Spinograptus* group (*S. spinosus*, *S. clathrospinosus*, *S. latespinosus*, *S. munchi*), in which complex, paired reticulofusellar processes of greatly varying length, width and complexity were developed on the upper apertural list (Fig. 3.10). Single complex, lacy reticular hoods also appeared in other taxa at this time (Lenz 1994a; Lenz – Kozłowska-Dawidziuk 2002b?) (Figs 3.6, 3.14).

In the Ludlow, the proliferating *Plectograptus* group and specifically *P. wimani*, developed single apertural processes of irregular, multifold loops (see Kozłowska-Dawidziuk 1995), and some species of *Neogothograptus*, a member of the *Gothograptus* group, produced complex, paired reticulofusellar processes on the upper apertural list (Fig. 3.17) (Kozłowska-Dawidziuk 1995; Lenz – Kozłowska-Dawidziuk pers. observation 2000). The youngest members of the *Gothograptus* group, *Holoretiolites* (Fig. 3.4), and of the *Plectograptus* group, *Semiplectograptus*, and *Plectodinemagraptus*, however, have much reduced skeletal lists and are without any kind of apertural process (Figs 3.7, 3.9).

It appears then, that the appearance complex apertural structures/genicular processes coincided with the development of the upper apertural list, a structure that appeared only in the early Homeric. By comparison, the *Sokolovograptus* and *Paraplectograptus* lineages that range into the early Homeric, lack upper apertural lists and are without apertural processes.

Stomata

Stomata along the lateral wall of the ancora sleeve are relatively common in the earlier retiolitids, being found in *Pseudoretiolites*, *Pseudoplegmatorgraptus* and, especially *Stomatograptus* (Figs 2.7, 2.8). The structure appears to have arisen again, possibly independently, in the early Homeric where it is found only in some species of *Cometograptus* (e.g., *C. apoxys*) (see Lenz 1993). Stomata are only rarely known beyond the post-*lundgreni* extinction event, as in the case of one specimen of *Spinograptus* sp. with preserved membranes (Fig. 2.3).

Ancora sleeve spines

These novel structures have been recently described as seamed spines present on the ancora sleeve of *Cometograptus* (Kozłowska-Dawidziuk 2001). The spines are located along the central part of the lateral wall of the ancora sleeve, and have outward-facing seams that are a continuation of the ancora sleeve list seams (Fig. 3.8).

Size

As already noted by Lenz – Melchin (1997), the retiolitids, in general, show an overall steady trend toward size reduction up the stratigraphic column. Taxa such as *Retiolites*, *Pseudoplegmatorgraptus*, and *Stomatograptus* sometimes exceeded 100 mm in length and 8–10 mm in width (see e.g., Bouček – Münch 1943; Lenz 1982); “mid-range” taxa such as *Sokolovograptus*, *Spinograptus*, *Gothograptus* and *Paraplectograptus* may attain 10–15 mm in length and two to three mm in width (Fig. 3.1); and “end-members” such as *Neogothograptus* and *Holoretiolites* are generally no more than 2 mm to 5 mm long and about one mm wide (Figs 3.2, 3.4, 3.16, 3.17).

The size trend is further illustrated in two examples. The *Gothograptus* lineage first appears in the early Homeric and continues to almost the highest range of the retiolitids. The early Homeric representative, *Eisenackograptus eisenacki*, as well as *G. nassa*, appearing in the earliest late Homeric, may possess as many as 19 pairs of thecae; simultaneously, however, some populations include forms possessing as few as three thecal pairs (Fig. 3.5). A younger member of that lineage, *Neogothograptus*, appearing in earliest Ludlow, possesses up to seven pairs of thecae and often fewer (Figs 3.16, 3.17); whereas the slightly younger *Holoretiolites mancki* may possess no more than two thecal pairs.

The *Plectograptus* lineage is further illustrative. The lower Ludlow forms, *P. macilentus* (Fig. 3.21) and *P. wimani* attained rhabdosome widths of about 2.5 mm; the succeeding *Semiplectograptus* attains about 1.7 mm in width; and the youngest member, *Plectodinemagraptus* is only about 0.7 mm wide. In all of the above reductions in size, there is a concomitant reduction first in reticular lists, followed by a reduction in ancora sleeve lists, which seems almost completely reduced in the last representative, *Plectodinemagraptus gracilis* (Figs 3.7, 3.9).

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Evoluční rozvoj silurských retiolitidních graptolitů

Retiolitidní graptoliti se v siluru objevují poprvé ve starší části aeronianu, a ve vyšším aeronianu až starším telychianu procházejí pozoruhodnou diverzifikací. V tomto časovém úseku se tak objevuje více než třicet druhů. Méně významný vrchol druhového rozvoje přichází ve spodním homerianu (biozóna *lungreni*) a předchází významnějšímu vymírání v průběhu této biozóny, jehož důsledkem bylo přežití jediného druhu. Poslední retioliti vymírají v průběhu biozóny *leintwardinensis* ve středním ludlowu. Na úrovni podčeledi jsou významné dvě vývojové změny. První představuje změnu od dovnitř obrácených švů na lištách na nástavci kotvičky a podélnou striaci nebo hladký povrch lišt (viditelných na většině starších taxonů) k dovnitř obráceným švům a hrbolkovitým povrchem lišt na stratigraficky mladších taxonů (tyto znaky jsou patrné v průběhu biozóny *lundgreni* a u všech mladších typů stratigraficky staršího rodu *Sokolovograptus*). Jinými vývojovými trendy v průběhu fylogeneze jsou: ztráta sikuly schopné fosilizace; více než dvojnásobné protažení sikuly; změlčení a podstatné zjednodušení záchytné kotvičky; redukce nástavce kotvičky; změna profilu téky od časně orthograptidního typu k pozdně climacograptidnímu typu. Dalším trendem je změna od nemy zcela přichycené k lištám k nemě přichycené pouze distálně, často na nástavci nebo ke vzniku úplně „volné“ nemy a k vývoji nástavce u mladších forem. Dalšími trendy jsou: přítomnost vnitřního nebo vnějšího nematularia pouze u forem s „otevřeným koncem“; vývin svrchní aperturální lišty ve spodním homeru se složitými aperturálními výběžky u některých forem; nápadné zmenšení velikosti od rabdozómů dlouhých více než 100 mm u stratigraficky časných forem na pouze 2–3 mm dlouhých rabdozómů u mladších typů; zjednodušení rabdozómu jako důsledek redukce tekálních a kotvičkových lišt doprovázený výrazným nárůstem délky sikuly.